Biology of *Dufourea* and of its cleptoparasite, *Neopasites* (Hymenoptera: Apoidea)

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Abstract: The biologies of four species of *Dufourea* [*D. mulleri* (Cockerell), *D. malacothricis* Timberlake, *D. pulchricornis* (Cockerell), and *D. trochantera* Bohart] are described and compared. The biology of the nomadine bee parasite, *Neopasites,* family Anthophoridae, is also described. Two species of the parasite are associated with their hosts [*Neopasites* (*Micropasites*) *cressoni* Crawford with *D. mulleri,* and an undescribed species of the subgenus *Neopasites* with *D. trochantera*]. The suspected association of an additional species, *Neopasites* (*Neopasites*) *fulviventris* (Cresson), on *D. dentipes* Bohart and an undescribed *Dufourea* species is included. The subfamilies of Halictidae are compared on the basis of biological features in a summary table.

The family Halictidae (composed of Halictinae, Nomiinae, and Dufoureinae) is well represented in the biological literature. Most of the information, however, concerns halictines and nomiines. Previous biological studies of the Dufoureinae have been restricted to six species within two Old World genera: *Rophites canus* Evers (Enslin, 1921; Malyshev, 1925a), *Rophites hartmanni* Friese (Malyshev, 1925a), *R. quinquespinosus* Spinola (Stockhert, 1922), *Systropha planidens* Giraud and *S. curvicornis* Scopoli (Malyshev, 1925b), and *S. punjabensis* Batra and Michener (Batra and Michener, 1966). The holarctic genus, *Dufourea*, has not been studied biologically, even though it is widely distributed and contains the greatest number of species in the subfamily. The biologies of four *Dufourea* species (*D. mulleri* (Cockerell), *D. malacothricis* Timberlake, *D. pulchricornis* (Cockerell), and *D. trochantera* Bohart) are reported.

The biology of the New World *Neopasites* (= *Gnathopasites*) is also described. It and its Old World counterpart, *Biastes*, comprise the nomadine tribe Biastini which are cleptoparasitic primarily on the Dufoureinae. *Biastes* attacks the nests of *Rophites, Systropha*, and presumably the eucerine *Tetralonia* (Popov, 1951), and *Neopasites* attacks those of *Dufourea.*

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Dufourea mulleri (Cockerell)

Description of Habitat: Bohart, Torchio, and Nabil Youssef studied the biology of this species at Tubac, Santa Cruz County, Arizona, between April

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Fig. 1. Nesting area of *Dufourea mulleri* (Cockerell) at 3 miles south-southwest of Rodeo, Hidalgo County, New Mexico.

13 and 17, 1965. Torchio returned to this site on April 27, 1965, and found nesting had been completed. On April 26, 1966, he revisited the nesting site and discovered the nesting population greatly reduced over the previous year. Rozen studied the species 3 miles S.S.W. of Rodeo, New Mexico (Fig. 1) (actually in Cochise County, Arizona), between May 1 and 5, 1965. Rozen and Favreau revisited this site between April 26 and May 5, 1966, at which time the species was more abundant and nested in various areas along the road between this point and Apache, Arizona.

The Tubac site was located adjacent to a gravelly creek bottom which carried water during short periods each year. *Phacelia* of two species, *Lesquerella, Malacothrix, Acacia greggii* Gray, a tall crucifer, and several grass species were the predominant plants growing along the creek. The surrounding area is typical of the Lower Sonoran. The Rodeo site, a recently disturbed, nearly flat area, half a mile long, was adjacent to a highway running in a S.S.W. direction through the wide San Simon Valley. The nest area was occupied by low, sparsely scattered herbs, including the pollen plant, *Phacelia popei* T. & G. var. *arizonica* (Gray) Voss, and a *Lepidium* species. The vegetation adjoining the nest area was dominated by *Prosopis* and other xerophilous plants. The soil surface at both nesting sites was unshaded and ranged from horizontal or nearly so near Rodeo to gently sloping (up to 15°) at Tubac. At Tubac, nesting took place in two soil types. One had a 6 mm. layer

of dry, loose powder covering a hard-packed, sandstone-like layer composed of brownish soil interspersed with large gravel particles. The hard-packed layer extended below the cell level and contained some moisture below 4.6 cm. The second soil type was light brown, coarsely grained, and loosely packed to 5 cm. below its surface. Large, extremely hard-packed clods found below the surface layer were separated from each other by air spaces or narrow bands of loosely-packed soil. The soil was dry until well below the cell level. The nesting site near Rodeo was sandy and loosely packed from its surface to a depth of 3–4 cm., below which it became hard-packed and pebble-free. Moisture at the cell level varied from slight to moderate, depending upon the depth. Soil temperatures recorded from this site at a depth of 10 cm. on April 24, 1966, were: 9:30 a.m., 69°F; 10 a.m., 69°F; 12:30 p.m., 78°F; 3:15 p.m., 80°F. The time is Rocky Mountain Standard time and the day was clear and warm.

Although nests were scattered over extensive areas at both locations, nest concentrations also occurred. The most dense concentrations numbered ½ nest/sq. ft. at Tubac and 4 nests/sq. ft. near Rodeo. Apparently, the species can be regarded as weakly gregarious. Only a single female occupied a nest.

Nest Architecture

ENTRANCE HOLE: Some nest entrances occurred in flat, bare ground, but more frequently they were at the lower edges of slight depressions or at the bases of pebbles or rocks. Soil excavated from the nests was deposited on one side of the entrance, forming an asymmetrical tumulus. The typical tumulus at Tubac was heart-shaped and measured 33 mm. long by 27 mm. wide. A weakly defined trail 4 mm. wide, 2 mm. deep, and 18 mm. long extended from the entrance hole to near the apical angle of the tumulus. It was formed as the female swept excavated soil away from the entrance while she backed away repeatedly over the same terrain. At the terminus of the trail, the excavated soil was kicked back and away with rapid, flicking leg movements. The tumulus was continually reshaped and enlarged throughout the period of nesting activity.

Entrances were generally kept closed at Tubac but remained open near Rodeo. Possibly the divergent behavior at each location is simply a reflection of adaptability to nesting in different soil types. At Tubac the very loose surface powder tended to fill the entrance holes each time bees entered or left. Returning foragers, however, were able to orient to their respective entrance holes very successfully. They literally dove into the powdered layer, as do some *Nomadopsis* species, and rapidly moved soil about until they found and entered their burrow. The soil near Rodeo was sufficiently granular and hard-packed to allow the entrance holes to remain open. Entrances always lacked turrets.

BURROWS: The main burrow, circular in cross section, was 3.5 mm. in diameter and descended in a meandering fashion. There were no obvious constrictions at or near the entrance hole. The burrow walls were not lined but, at least at the Tubac site, they appeared darker in color and were more tightly packed than the surrounding soil. Their permeability to water was equal to that of the surrounding soil. A vestibule measuring 7 mm. in diameter was found in one nest at Tubac. It was constructed as a pocket in the wall of the main burrow 11 mm. below the soil surface. The main burrow was never plugged and it terminated in a nearly horizontal cell.

Lateral burrows were originated along a 15 mm. zone about halfway down the main burrow. The unlined laterals (as many as 9 per nest) radiated horizontally from the main burrow for distances ranging from 5 to 38 mm. Circular in cross section, they had the same diameter as the main burrow except where they narrowed to 3 mm. just before joining the cell. Each lateral was plugged tightly before a new one was excavated.

CELLS: The cells (Figs. 2–6), which were ovoid and broadly rounded distally, were placed from 10 to 40 degrees from the horizontal with the anterior end highest. Their length varied from 6.0 to 8.0 mm. and their width from 4.5 to 5.0 mm. They were carved from the surrounding soil and their inner surfaces had no apparent "built-in" wall. They were, however, lined with a dull varnish that was nearly transparent upon drying. This lining, less than 0.05 mm. in thickness, filled the space between the sand grains and could not be peeled from the walls of their cells. The lining permitted a moderately rapid absorption of water when a droplet was placed on it. At the Rodeo site a very thin layer of dull, extremely fine, silt-like material coated the depressions between the grains of sand. Cells were located between 5 and 10 cm. from the ground surface, with the uppermost cell being excavated first and the lowermost cell last. Cells from previous years were not reconditioned and reused.

The unlined cell cap was composed of a moderately packed soil plug which had 3 indistinct spiral rings and a small central micropyle on its concave inner face.

Although only one cell per lateral burrow was found at Tubac, two cells (and in one case, three cells) in linear series were commonly found at the end of the lateral burrows near Rodeo. The passage between these cells varied in length from 2.0 to 5.0 mm., and was filled with rather loosely packed soil between the firm rear wall of one cell and the firm cap of the other.

Provisioning and Development

D. mulleri provisioned its nests with pollen from two *Phacelia* species at Tubac. One species produced blue pollen and the other, yellow. Since the pollen balls were always either one color or the other, it appears that the bees visited only one host plant species while provisioning a cell. *Phacelia popei* T. and G.

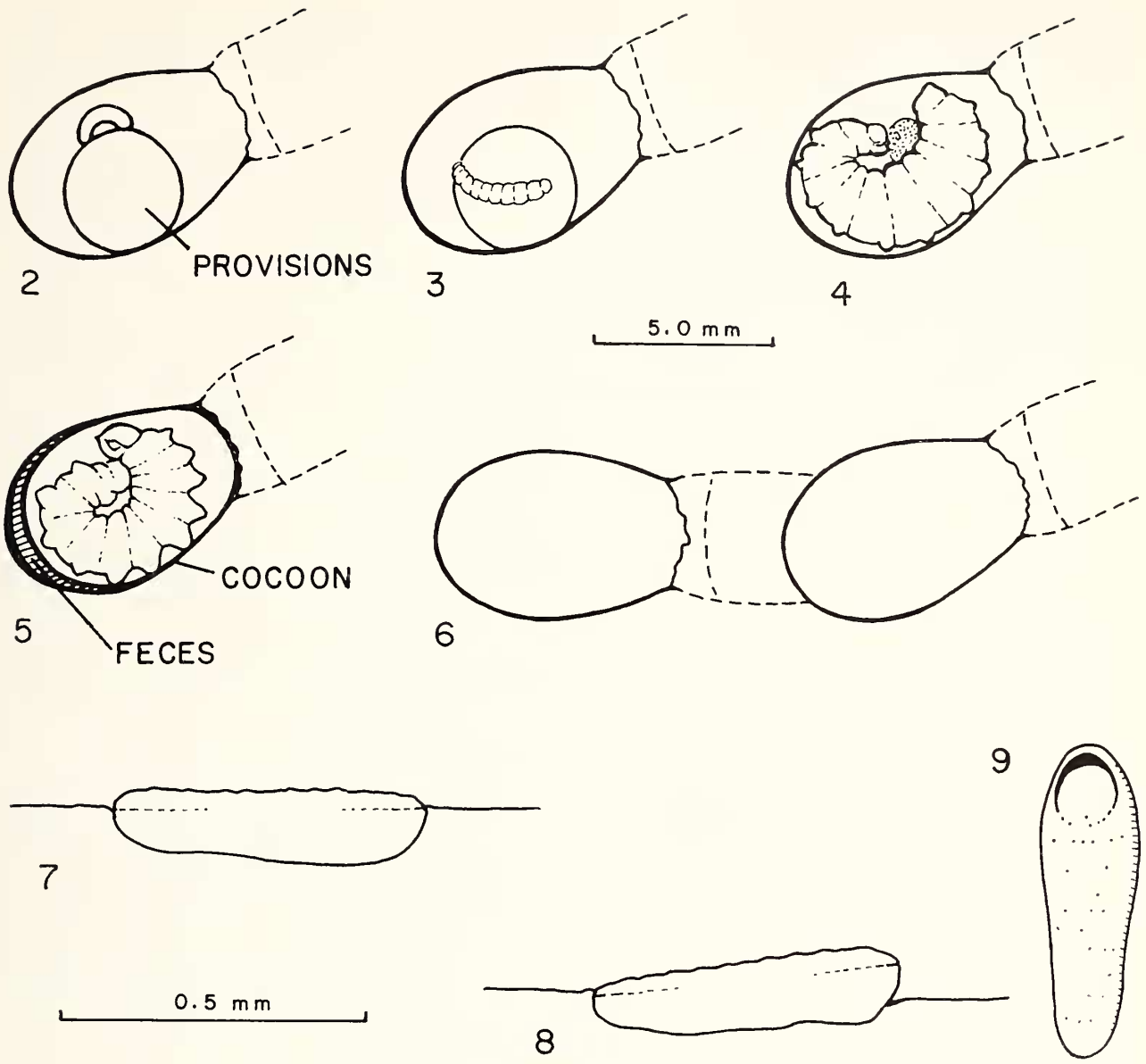
var. *arizonica* (Gray) Voss was the only pollen host near Rodeo. Its dry pollen remained bluish in color while on the bee's scopae but changed to lavender after it was molded into the provisions. The color of the pollen ball faded to a light tan by the time the first instar hatched from the egg.

Approximately three pollen loads were required to complete one pollen ball. The first load, after being transported to the cell, was mixed with nectar and shaped into a small but complete sphere. Each additional load was added to the existing sphere until it became a moist but firm, homogeneous, spherical ball, averaging about 3.5 mm. in diameter and ranging from 2.75 to 3.75 mm. The ball was placed near, but not at, the posterior end of the cell (Fig. 2). The pollen balls of this species resembled those of the panurgine genera *Nomadopsis* and *Calliopsis* in shape and consistency, but lacked a waterproof covering.

The shiny, whitish, strongly arched egg (Fig. 2) was approximately 1.9 mm. long and rested on top of the provision in the sagittal plane of the cell. Both ends were weakly attached to the provisions so that eggs were easily displaced when cells were excavated. In contrast, the eggs of some bees (e.g., certain Panurginae) are attached securely by their posterior ends while the anterior tip rises in the cell or merely touches the provision. In *mulleri* the broader anterior tip of the egg faced the cell closure.

Immediately before the first instar hatched, the egg chorion adhered to the embryo, so that the rather small head and body segmentation were visible on the still strongly arched egg. After hatching, the larva fed and crawled about on the provisions (Fig. 3). The first-stage larva, as well as subsequent ones, was equipped with a pair of dorsolateral tubercles on most body segments, with a somewhat protruding venter on the ninth abdominal segment, and with a posterodorsally directed tenth abdominal segment which could be contracted and expanded somewhat. These modifications assisted the larva as it crawled; by appressing the protruding ninth segment to the pollen ball and the expanded tenth to the cell wall, the larva stationed the posterior part of the body so that it could push its front part forward. While moving forward and bending the anterior portion of its body up and down, the larva fed on the pollen ball and left a wide, shallow groove in its wake. Because the feeding larva circled its provisions in random directions, the ball remained nearly spherical almost until it disappeared (Figs. 3–4).

After consuming the pollen ball, but before defecating, the larva began spinning a cocoon which, when completed, tightly adhered to the cell walls. When the outer layer of the cocoon was completed, the larva extruded long semi-moist, pale yellow fecal pellets which were applied to the posterior one-half to two-thirds of the cocoon in short strips more or less parallel to the long axis of the cell. During or after the late stages of defecation, the larva applied additional silk over the inner face of the outer cocoon layer and feces



Figs. 2–6. Cells of *Dufourea mulleri* (Cockerell): 2. With pollen ball and egg, side view. 3. With pollen ball and young larva, side view. 4. With nearly mature larva, side view. 5. With postdefecating larva, cocoon, and feces, side view. 6. In linear series, top view.

Figs. 7–9. Eggs of *Neopasites* (*Micropasites*) *cressoni* Crawford: 7. Embedded nearly flush with cell wall, lateral view. 8. Embedded at an angle with cell wall, lateral view. 9. After hatching, showing semicircular split at anterior end, dorsal view.

until a complete inner cocoon layer was formed. This very thin inner layer completely isolated the larva from its feces. Most of the fecal pellets, although flattened into ribbons by the pressure of the larva, were still distinguishable.

The completed cocoon (Fig. 5) was composed of two layers and assumed the same shape and dimensions as the cell. The parchment-like outer layer was dull, light brown on both of its surfaces but somewhat darker across its anterior face, where it was thicker. The inner layer was composed of a clear matrix interspersed with silk strands. It was very thin and tightly appressed to the inner face of the outer layer except where it incorporated and covered the fecal cake. The exposed surface of this layer was glossy. The cocoon was not

supplied with a nipple, but individual thread-like silk strands were detected. Soft and easily collapsed anteriorly, it was more rigid where the feces gave it additional support.

After the cocoons were spun, cells were difficult to find because they no longer broke open easily during excavation. Although the cocoons imparted extra strength to the cells, the mature larvae may also have secreted a hardening substance that permeated the soil adjacent to the cell. In any event, the wall of a cell occupied by a cocoon seemed much tougher than that of a cell containing an egg, an early instar, or an immature of *Neopasites,* which does not spin a cocoon.

Adult Activity

D. mulleri and *Neopasites cressoni* Crawford began flying between 9:00 a.m. and 9:30 a.m. M.S.T. on a warm clear day, and were still active at 2:30 p.m. Males of *D. mulleri*, presumably in search of mates, were often seen flying swiftly from host plant to host plant. Mating, observed only once, occurred near some host plants and was completed in 5 seconds. The bees did not fly *in copula* and mating was never observed at the nesting site.

Associates

Eurystylops (Strepsiptera) was discovered at Tubac as mature females in the abdomens of adult bees and as first instar larvae on the eggs. In one area of the same site, 90 percent of the bee cells contained dead first instars and were infested with a mold complex, including the genus *Rhizoctonium*.[3] The biology of *Neopasites cressoni*, which attacked *D. mulleri* at both nesting sites, is described near the end of this paper.

One burrow of *D. mulleri* possessed a unique feature in that it branched at the 2.5 cm. level. The branch, 2.5 mm. in diameter, led to two somewhat smaller cells containing a predefecating and a postdefecating larva belonging to the panurgine genus *Perdita*. They may well have been *Perdita sexmaculata* Cockerell, as this species was the only one abundant in the area at that time. Although the *Dufourea* female was still provisioning its part of the nest whereas the *Perdita* was not, it is impossible to say which had first started the nest because some offspring of both females had become mature larvae.

Dufourea trochantera Bohart

Description of Habitat

This species, which is closely related to *D. mulleri*, was discovered by Torchio nesting gregariously at Newton Dam, Cache County, Utah, on May 27, 1966. The nesting site was located on a 10-foot high, south-facing embankment inclined about 55° from horizontal. The site was made available recently when two

[3] Identified by G. M. Baker, Botany Dept., Utah State University.

roads converging near the nesting site were cut below the natural terrain of the hillside leading to the reservoir. Nests were mostly confined to an unvegetated 10-foot wide area of the embankment, and most entrances were situated toward the crest of the slope. A few nests were established at the top edge of the embankment where the grade was almost horizontal.

Flowering plants growing in the vicinity of the nesting site were: *Cirsium lanceolatum* (L.), Hill, *Oenothera* sp., *Brassica* sp., *Sphaeralcea* sp., *Salix* sp., *Penstemon* sp., and *Phacelia leucophila* Torr. *D. trochantera* was utilizing *Phacelia leucophila* as its pollen and nectar source.

The surface layer of the nesting site was composed of a fine, black powdered soil, ranging from 5 to 10 mm. in depth. Below this the black, clay soil became extremely hard-packed and contained numerous pebbles and rocks of varying sizes. The soil was dry to below the cell level.

Nest Architecture

ENTRANCE HOLE: Entrance holes were inclined at 45° angles from the horizontal regardless of the slope characteristics. All entrances, including those on the horizontal surface, faced south to southwest and were kept open. At times, however, winds disturbed the surface layer sufficiently to cause closure of some nests. Returning females associated with these nests landed near the plugged entrances and dug until the burrows were re-exposed.

Nesting females kicked excavated soil from the entrances of nests located on steep slopes until indistinct tumuli were deposited below the nests as long strips of soil. If entrances were located on the horizontal surface, each nesting female dragged excavated soil from the nest repeatedly over the same course until a trough or trail was formed. A typical tumulus measured 36 mm. long and 13 mm. wide. The trough was 3 mm. wide and extended about half the length of the tumulus. No obvious constriction or expansion of the burrow occurred at or near the entrance hole.

BURROWS: The unlined, unplugged main burrows were 3.5 mm. in diameter. They descended to depths ranging from 3 to 5 cm. When unobstructed, they spiraled downwards but were often forced to detour around pebbles and rocks. In two of the 25 nests excavated, an unlined vestibule was placed as a carved outpocket on a sharp turn of the main burrow. One of these measured 14 mm. wide by 9 mm. deep, and the second measured 7.5 mm. in diameter.

The lateral burrows were also unlined and of the same diameter as the main burrow. They originated along the main burrow at different points and meandered for distances of 4 to 42 mm., where they terminated at cells between 5 and 10 cm. below the surface. The laterals were tightly plugged after the cells were capped. We were unable to determine whether the main burrow terminated at a cell and was subsequently plugged for several centimeters or whether it divided into two or more laterals that were eventually plugged.

CELLS: Cells of this species were remarkably similar in shape, form, and manner of construction to those of *D. mulleri*. The cell lining differed from that of *D. mulleri* in its somewhat greater impermeability to water.

The cell cap, 3 mm. in diameter and composed of a moderately well-packed soil plug, was slightly concave. The unvarnished inner face had two to three indistinct rings surrounding a central micropyle, while the flat outer face had a smooth, unvarnished surface.

Most of the lateral burrows terminated at single cells, but others (about 25 percent) led to two cells in linear series. The cells were usually subhorizontal but sometimes dipped to as much as 30° below the horizontal. The passages between those cells in linear series were plugged with soil that varied from loosely to tightly packed.

Provisioning and Development

The provisions of this species were similar to those of *D. mulleri* except for their tan color and slightly smaller average size (2.85 to 3.25 mm.).

The eggs appeared to be slightly smaller than those of *D. mulleri* (1.8 mm. long by 0.4 mm. wide) but the samples may have been too small for a reliable comparison.

Embryonic development, hatching, and larval shape and mobility all appeared to be identical with the same features in *D. mulleri*.

Cocoon formation and structure were quite similar to those of *D. mulleri*. However, the following differences appeared to be consistent: (1) The outer cocoon layer was somewhat thicker and darker brown toward the anterior end, and there was a very thin, translucent zone about 2 mm. wide anterior to the fecal cake; (2) the fecal pellets composing the fecal cake were more completely fused into a single sheet.

Adult Activity

During warm, sunny weather, *D. trochantera* began flying at about 8:30 a.m. M.S.T. By 1:30 p.m. almost all flight ceased. Pollen loads were acquired in from 5 to 18 minutes and the time spent within the nest between loads varied from 2.5 to 36 minutes. This variation in time spent in the field and within the nest appeared to have no correlation with the time of day.

Associates

In the course of about 15 hours of observation at the nesting site, only two adults of an undescribed species in the subgenus *Neopasites* were seen. Surprisingly, four of the approximately 40 host cells examined contained quiescent, postdefecating larvae of the parasite. The limited biological information obtained agreed with that of *Neopasites cressoni* discussed in a separate section below. One cell of *D. trochantera* contained four dipterous larvae which were consuming the provision. Unfortunately, this cell was lost in transit from the field to the laboratory.

In 1962 a series of *Neopasites* adults were collected at a *D. trochantera* site on the Independence Lake Road, Sierra County, California, by M. E. Irwin. We compared specimens from both the California and Utah sites and found them to be distinct but undescribed species.

Dufourea malacothricis Timberlake

This species, smaller than *D. mulleri,* was collected from flowers of *Malacothrix* near Rodeo between April 26 and May 5, 1966. It was somewhat less common than *D. mulleri,* with which it flew, and only two nests were discovered by Favreau and Rozen, one at the Rodeo site (described above) and the other in an open area 3 miles north of Apache, Cochise County, Arizona.

Nest Architecture

ENTRANCE HOLE AND BURROW: The nest entrance and main burrow near Rodeo remained opened and bore an asymmetrical tumulus. The main burrow was 2.25 mm. in diameter and meandered a short distance before it was lost in the excavation.

The second nest occurred on unshaded, nearly horizontal terrain with a 2 cm.-deep surface layer composed of rather loosely packed soil. The soil below was compacted sand free of pebbles. The cells were 10 and 12 cm. deep where the soil was moist. The unlined main burrow, 3.0 mm. in diameter, descended in a meandering fashion to a number of unlined and completely plugged lateral burrows of the same diameter. These laterals were horizontal or somewhat descending and were 4.0 to 4.5 mm. long, although one extended 10 mm.

CELLS: Twelve cells were uncovered from the seven laterals associated with the one nest. Two cells were placed singly and the other 10 were grouped into linear series of two each. The distance between pairs in a series varied from 1.0 to 2.0 mm. All cells were inclined from 10 to 15 degrees from the horizontal with the rear of the cell lower than the front. They were identical in shape to those of *D. mulleri* and had the same type of lining and construction. The lining, however, was even less waterproof than that of *D. mulleri* in that it almost immediately absorbed a droplet of water. Cells varied from 5.0 to 5.5 mm. in length and from 3.5 to 4.0 mm. in maximum diameter. They were closed with a spiral plug, as in the case of *D. mulleri,* and the oldest cell was closest to the surface.

Provisioning and Development

The pollen balls of *D. malacothricis* differed from those of *D. mulleri* only in being yellow and in having a smaller diameter (2.75 to 3.0 mm.). The smaller eggs (1.75 mm. long) were identical in shape and placement with those of *D. mulleri,* and developing larvae practiced the same feeding habits. Unfortunately, no cocoons of this species were obtained.

Associates

The one nest excavated was free of parasites and predators even though *Neopasites cressoni* occurred in the area.

Dufourea pulchricornis (Cockerell)

Description of Habitat

Bohart and Torchio found this species collecting pollen from *Lesquerella gordoni* (A. Gray) Wats. on the edge of a dry creek bed 14 miles E. of Tucson, Arizona, on April 12, 1965. One active nest was located on a small sandy strip near the center of the gravelly creek bottom. The uneven surface of the strip was sparsely covered with grass and about 10 percent of it was covered by driftwood and other flotsam.

Nest Architecture

ENTRANCE HOLE: The nest was located near the base of several converging grass plants but it was reasonably well exposed. The burrow entrance was open, faced west, and angled into the soil surface. A small bell-shaped enlargement surrounded the entrance to several millimeters below the surface but it was probably an abnormal structure caused by the collapse of the adjacent, loose, dry sand and its subsequent removal by the nesting bee.

A well established asymmetrical tumulus, continually reshaped and enlarged by the nesting female, was present in front of the entrance hole. A shallow trail, 4 mm. wide, extended 3 cm. from the entrance, whereupon it made a 90° turn to the north and continued for an additional 8 mm. The moraine on either side of the trail was quite wide (8 mm.) and contained many pebbles and large sand particles. The trail and associated moraines of the tumulus were formed in the manner described for *D. mulleri*.

BURROWS: The main difference between the burrow system of *D. pulchricornis* and that of other species of *Dufourea* described here was the subdivision of lateral burrows into sublaterals. Unfortunately, the only nest available for study was incomplete and portions of the architecture were lost during excavation. Nevertheless, architecture differed sufficiently to justify description here.

The main burrow was unlined, unplugged, and 3 mm. in diameter. It maintained about a 20° angle from horizontal for 10 mm., whereupon it made a subhorizontal spiral and proceeded vertically. It branched into two lateral burrows about 7 mm. below the surface, but one branch was soon lost. The remaining lateral was difficult to follow because it was partially plugged (possibly in the process of being completely plugged), but it eventually divided into a number of plugged sublaterals radiating short distances from the lateral burrow. Each sublateral terminated at a single cell. The four cells eventually uncovered were 9 cm. below the surface and positioned 3 to 4 mm. apart.

CELLS: The cells were subspherical (5.75 mm. long and 5.0 mm. wide) and varied in position from subhorizontal to a 70-degree inclination from horizontal

with the posterior portion lower. As in the other *Dufourea* studied, the cells were carved from the substrate, but they lacked water-resistant walls as determined by the droplet test.

The cell cap was composed of an unlined, tightly-packed soil plug 3.5 mm. wide and 3.0 mm. long. The inner face of the plug was concave and possessed three distinct rings surrounding a 1 mm. wide, central micropyle. The outer face of the cell plug could be distinguished from the plugged sublateral burrow only by its greater compaction.

Provisioning and Development

The pollen ball closely resembled that of *D. mulleri* in shape and diameter but differed in being yellow and somewhat drier. In subhorizontal cells, the pollen balls were positioned as were those of *D. mulleri* but they were at the bottom of the more vertical cells.

Adult Activity

The female whose nest we studied completed three pollen-carrying trips between 10:30 and 11:07 a.m., and began a fourth trip at 11:10 a.m. The speed with which she collected pollen and deposited it into a cell was remarkable, considering that the day was overcast and the air temperatures never rose above 70°F. From the above data, it appeared that each pollen ball required at least four pollen loads for its completion.

Approximately 100 pollen-collecting females were observed between 8:30 and 9:30 a.m., but an hour's search throughout the area yielded but one nest. Consequently, *D. pulchricornis* was not gregarious under the conditions we encountered.

Neopasites (*Micropasites*) *cressoni* Crawford

Flight Activity

This species of nomadine parasitic bee was encountered both at the Tubac site and at the Rodeo site. The females, more abundant than the males, flew low over the ground in a meandering fashion. They began flying as early in the day as their hosts and continued after the hosts ceased. Their flight, suggestive of that of *Oreopasites* and *Holcopasites*, was moderately slow and included frequent stops at apparent nest entrances of the host bee. Several times, two, three, four, or even five females hovered over a nest entrance, though such congregations occurred only where the cuckoo bees were most numerous. They often landed on flat, unshaded surfaces, probably to rest or sun themselves. Males were seen several times at the Rodeo site; their flight was higher and seemed somewhat faster than that of the females.

Mating was not observed, but one of us (Torchio) observed it in *N.* (*Neopasites*) *fulviventris* Cresson at Arroyo Seco, Monterey County, California, in

1959. The males utilized a small, bare, powdered surface area as a gregarious mating site. It was separated from the nesting area of its suspected host, *Dufourea dentipes* Bohart, by about 21 meters. Males patrolled the area or landed on it for long periods. Mating was observed in four instances, each occurring on the ground. Copulation lasted from 3 to 10 seconds.

Oviposition

Over 30 eggs and egg chorions of *N. cressoni* were encountered in cells of *D. mulleri* at the Rodeo site (by Rozen and Favreau), and all except one were deposited in the cell wall, as is the case with the other nomadine parasitic bees whose biology has been studied. Only once was an egg discovered embedded in the provisions; as there were already six eggs in the wall of this cell, we can only imagine that the female responsible for the seventh egg might have been at a loss to know what to do with it.

It is not known how many eggs are normally deposited in a cell; usually one or two were discovered though as many as eight were found in a single cell. The last figure may be abnormally high, for the female *Dufourea* probably left the cell open, thereby giving numerous *Neopasites* access to the cell. Frequently deep, rough scratches were observed in a cell which suggested that the host female, upon finding the *Neopasites* eggs in the cell wall, dug them out; Rozen has observed similar marks in the cell wall of *Nomadopsis* in areas infested with *Oreopasites*.

Eggs were deposited while the cells were being provisioned. The female *Neopasites* made a groove in the cell wall and inserted the egg, so that it rested with its exposed length flush with or a little higher than the cell wall (Fig. 7). Occasionally the egg was tilted at a slight angle so that one end projected farther than the other (Fig. 8). In all cases the lining of the cell abutted the egg, so that there was never a crack between the cell lining and the egg. This fact indicated that the female *Neopasites* cemented the crack with fine soil, and, in certain cases, some cement-like material adhered to the exposed part of the egg. The eggs seemed to be placed in almost any part of the cell though they were not ordinarily found near the entrance.

The small eggs (Figs. 7–9) had an unusual appearance. About 0.6 mm. long, they were elongate, with the exposed surface being somewhat flattened, whereas the embedded part bowed out; they were thus rather boat-like in shape. The exposed chorion was stiff, thick, opaque white with faint, transverse corrugations. The chorion below the cell surface was thin, fragile, transparent and without ridges. At hatching, the exposed chorion ruptured (Fig. 9) in a semicircular to nearly circular line at the anterior end of the egg and the first-stage larva crawled out, leaving the chorion and attached door intact.

Like the egg, the first-stage larva was very small, being considerably less than half the size of the *Dufourea* egg. The head was conspicuous, con-

Table 1. The three subfamilies of Halictidae compared on the basis of known biological differences.

Subfamily	Entrance of nest burrow constricted	Cell lined with soil	Cell lined with secretion	Cell elongate	Cell asymmetrical	Cell horizontal or slanting (not vertical)	Provision shaped from first pollen load	Provision spherical	Provision retains shape throughout consumption	Larva motile	Cocoon present	Overwinters as fertilized female	With social representatives	Some cleptoparasitic
Dufoureinae	−	−	+−	−	−	+	+	+	+	+	+	−	−	−
Halictinae	+	+	+−	+	++−	++−	−	−	−	−	−	++−	++−	+
Nomiinae	+	+	+	++	−	−	−	−	−	−	−	+—	+—	−

stricted behind, and possessed elongate sharp-pointed mandibles. The tip of the abdomen was a bilobed pygopod-like structure used for crawling. These active larvae destroyed the host egg (or perhaps early stage larva) and also their siblings so that only one parasite larva survived in a cell.

The older larvae of *Neopasites* (Rozen, 1966) appeared rather similar to those of their host because of the elongate body form and because of the protruding ninth abdominal venter and the somewhat dorsally projecting terminal segment. However, it lacked dorsolateral tubercles, and therefore could be easily distinguished from its host. Like the host larva, it wandered over the pollen ball and fed, after which it defecated. At least in some instances, not all of the provisions were consumed. The feces were deposited on the wall toward the lower rear of the cell. A cocoon was not spun; the rigid, quiescent larva overwintered.

Although the undescribed *Neopasites* associated with *D. trochantera* from Utah was not observed as thoroughly as *N. cressoni*, its biology (as deduced from the fecal pattern, shape of pollen residue, adult searching behavior) and the gross appearance of the larvae did not appear to differ.

DISCUSSION

Two of us (Torchio and Bohart) have attempted to analyze the systematic relationship of the three subfamilies of Halictidae on the basis of available biological data (Table 1). Limited biological information on three genera of Dufoureinae (*Rophites, Systropha*, and *Dufourea*) indicates that this is a homogeneous and distinctive taxon. Of the three subfamilies of Halictidae, the adults of the Nomiinae are the least diverse structurally. Nevertheless, as indicated in Table 1, the Dufoureinae are equally homogeneous biologically. The Halictinae, with the most diverse biological characteristics, are, as adults, comparable to Dufoureinae in structural diversity. The distinctiveness of the

Dufoureinae is apparent from the number of biological characteristics by which it differs from the other subfamilies (Table 1). On the basis of these characteristics, it would appear that the Halictinae and Nomiinae are more related to each other than either is to the Dufoureinae.

When the genus *Dufourea* is revised, the four species discussed in this paper will probably be placed in two subgenera, *D. malacothricis* in one and the other three species in another. Of this second group, *D. mulleri* and *D. trochantera* will be treated as closely related species and *D. pulchricornis* as a more distinctive form. However, these two subgenera have a closer affinity to each other than do more divergent subgenera as represented by such species as *D. spinifera* (Viereck) or *D. maura* (Cresson).

If biological characteristics always verified species relationships based on morphological features, one would expect *D. malacothricis* to demonstrate the most unique nest architecture of the four species discussed. The nest of *D. pulchricornis*, however, is the most distinctive since it is the only species with sublaterals and unlined cells. As might be expected, the biologies of *D. mulleri* and *D. trochantera* are very similar.

Neopasites appears to be a specific parasite on Dufoureinae, but specificity within the genus is incomplete (i.e., *N. fulviventris* on *D. dentipes* and an undescribed *Dufourea* species).[4] Furthermore, at least two undescribed species of *Neopasites* are known to parasitize one *Dufourea* species (*D. trochantera*). Biological similarities within both the host and parasite genera may account for this, although more information is obviously needed.

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[4] R. M. Bohart, R. O. Schuster, and R. Brumley collected *N. fulviventris* adults at a nesting site of *Dufourea* n. sp. on April 8, 1966, in Jacolitos Canyon, 3 miles south of Coalinga, Fresno County, California.